

Dinosaur Tracks and Traces

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Dinosaur Tracks and Traces: An Overview

MARTIN G. LOCKLEY AND
DAVID D. GILLETTE

The journey of a thousand miles begins with a single step.
Lao Tse

Dinosaurian trace fossils are an extremely important if hitherto neglected branch of vertebrate ichnology; they generally provide information that is very different from that furnished by body fossils — information which is often not directly available from fossilized skeletal material. Like dinosaur skeletal remains, dinosaur tracks and traces — including footprints, eggs, nests and coprolites — have a world-wide distribution. Footprints are currently known from all continents except the Antarctic. Although sites yielding egg and nest remains are less numerous, they are almost as widely distributed. On the other hand, the distribution of coprolites is poorly documented (Fig. 0.1).

Footprints, nests, undisturbed eggs and coprolites represent in situ evidence of the dynamic activity of dinosaurs during life. Footprints can tell us approximately how many animals were present in a particular area, the directions they moved in, their relative abundance, size, and speed. They can also, like eggs and nests, reveal information about specific ancient environments and ecologies.

Identification of the trackmaker is one of the main objectives of tracking and it is often possible to identify trackmakers at the family level, as with footprints attributed to hadrosaurs or ceratopsians. In some cases a generic level identification is implied, as with the frequent designation of *Iguanodon* tracks. However, it has not yet been demonstrated that particular species of dinosaur can be identified from footprints with unique characteristics.

It is important to exercise caution in this endeavor and recognize the clear distinction between taxonomy based on skeletal remains and ichnotaxonomy based on track morphology. The considerable progress in tracksite documentation in recent years has led to significant improvement in this area and many mistakes in trackmaker identification have been rectified. Furthermore, even though trackmakers may not be identified below the family level, tracks often provide information on the morphology of hands and feet (mani and pedes) that is not available from the skeletal record. Similarly, recently advances in our understanding of the relationship between nests, eggs and skeletal remains has led to radical progress in our ability to interpret the affinity of eggshells and the behavior of

dinosaurs at nest sites (Horner 1987, Horner and Weishampel 1987, Mohabey 1987). It is also clear that coprolites are very abundant in some deposits (Jain this volume) and could benefit from systematic study.

At the present time dinosaur ichnology is making a significant number of new contributions to our understanding of dinosaurs and their habitats. Paleobiologists and restorers rely increasingly on trackways for authentic information on locomotion, stance and gait (e.g., Wade this volume), leading to radical reinterpretation of outdated reconstructions and exhibits. Nest sites and multiple parallel trackways are providing new insights into dinosaur social behavior and gregariousness (Sections IV and V herein). Regional scale synthesis of dinosaur tracks and traces shows a remarkable potential for suggesting temporal and spatial patterns of stratigraphic paleoecological and paleobiogeographic distribution of dinosaur faunas (e.g., Demathieu, this volume, Pittman this volume, Leonardi this volume, Lockley and Conrad this volume). As information emerges to suggest answers to other paleobiological issues, new questions arise. How important are experimental studies with modern trackmakers (Section VII)? How well do we understand the sedimentological context and preservation of tracks and nest sites (Section V)? And where does dinosaur ichnology go from here, after the rapid resurgence of the field in the last decade (Chapter 50)?

As the first comprehensive book ever compiled on dinosaur tracks and traces, this volume suggests various approaches, interpretations and answers, both to these new questions and to longer standing paleontological questions previously addressed without recourse to the burgeoning ichnological record.

Historical Perspective and Current Status

Early in the nineteenth century when dinosaurian and other Mesozoic tracks were first discovered in Europe and eastern North America, they were considered remarkable and important. As shown by the classic work of Hitchcock (1858), they were accorded much serious scientific attention, and the leading paleontologists and geologists of the day, including Owen, Huxley, Murchison and Lyell,

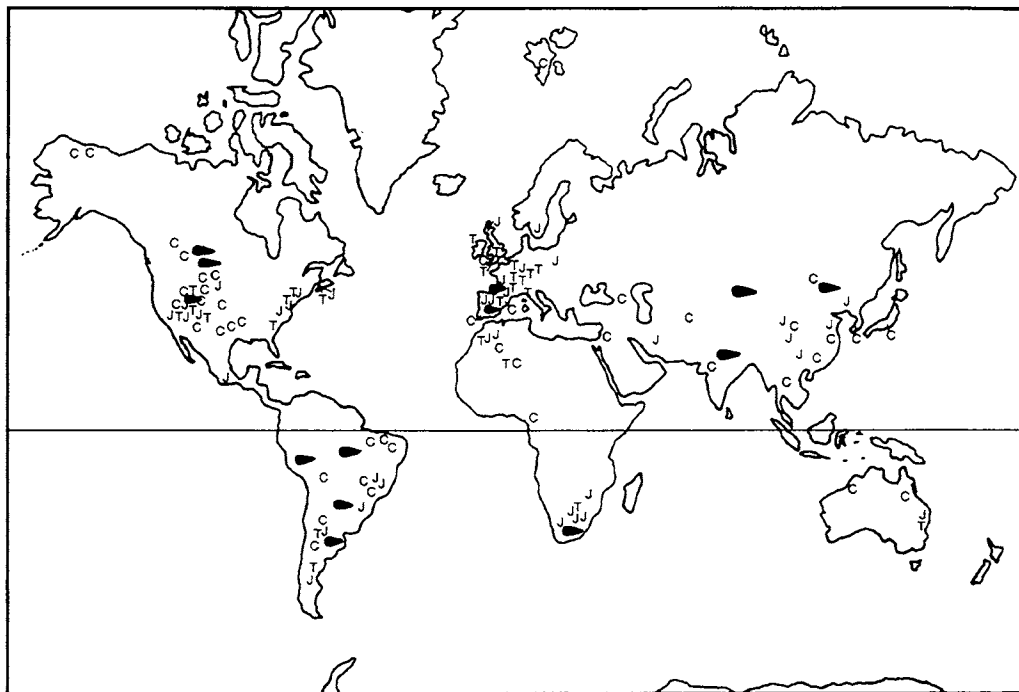


Figure 0.1. Global distribution of main dinosaur footprint sites and main dinosaur egg/nestsites.

T = Triassic, J = Jurassic and C = Cretaceous tracksites. Egg symbol represents dinosaur egg and nestsites.

all took a keen interest in their documentation and interpretation. Following Hitchcock's death in 1863, research in his field declined and, while our knowledge of dinosaurs began to increase dramatically, ichnology was generally neglected.

There is a perception that much of the early work was misleading or wrong; dinosaur tracks were identified as those of birds (*Ornithichnites*), a "mistake" which undermined the validity of ichnology, especially in the crucial area of trackmaker identification. Generally such a view is unfounded. Hitchcock and some of his contemporaries produced careful work which was exemplary in many respects, and, except in a minority of cases, much of the work, until comparatively recent times, was shoddy by comparison. The inference that three-toed dinosaur tracks were made by birds was *not* a result of thoughtless comparisons with modern tracks. Many early workers were well aware of the pitfalls of such a superficial approach, and only leaned towards suggesting avian affinity when large fossil birds like the "Moa" (*Dinornis*) and elephant bird (*Aepyornis*) were discovered. Knowing now what we do about dinosaur-bird relationships, the judgments of these early workers should not be called into question unduly, especially considering that dinosaur skeletal remains were then virtually unknown. If we accept that taxonomic categories like *Ornithischia* and *Ornithomimidae* are firmly established and that the theropod-bird connection is widely accepted, Hitchcock and his contemporaries were essentially correct in their interpretation of tracks from theropod-dominated footprint assemblages.

Perhaps it was the dramatic increase in discoveries of dinosaur skeletal remains which directed workers away from ichnology through the end of the nineteenth century and through the middle of the twentieth century. In any event, apart from the celebrated Mongolian egg discoveries of the 1920's and a minor flurry of activity associated with the discovery of important footprints in North America in the 1930's (Sternberg 1932, Brown 1938, Bird 1939), until recently, there has been little sustained resurgence of interest in dinosaur ichnology.

Consequently the recent dramatic increase in research activity on dinosaur footprints and nestsites is entirely without precedent. It is in part a facet of the general renaissance in all aspects of dinosaur research and in part a result of advances in the study of ancient terrestrial lithosomes and ichnology in general.

A survey of known dinosaur tracksites indicates that many hundreds are known. In areas where ichnologists have compiled locality data in a systematic fashion, reliable statistics are readily available. In the New World for example, recently compiled statistics indicate that at least 400 tracksites are known. These are distributed as follows:

Region	Approximate Number of Sites	Reference
Western Canada	~ 30	Currie this volume
Colorado Plateau region	~ 200	Lockley and Conrad this volume
Texas	~ 40	Pittman this volume
Eastern seaboard	~ 100	miscellaneous
South America	~ 40	Leonardi this volume

In the Old World a high concentration of sites has been documented in northwest Europe. These include the many Triassic sites, some without actual dinosaur tracks, researched by Demathieu, Haubold, Sarjeant and other leading ichnologists. In Africa a number of classic footprint-rich Late Triassic–Early Jurassic sites were documented from the Stormberg Series in the southern part of the continent (Ellenberger 1972, 1974; Olsen and Galton 1984). In the northern part of the continent somewhat younger Jurassic sites have been well-documented in recent years (Montbaron et al. 1985, Ishigaki this volume). In Asia there are a disproportionately small number of sites for the large land area. However, though very few sites are known for the Soviet Union, at least one appears to be very large and extensive (Romashko 1986), and in China, where research in this field is on the increase, over twenty-five sites are now known (Zhen et al. this volume). In the last decade sites have also been discovered for the first time in Korea (Lim et al. this volume), Japan (two papers herein) and Thailand (Buffetaut et al. 1985). There is also a low density of tracksites in Australia although the intensively studied Winton site has become very well-known (Thulborn and Wade 1984, this volume).

A survey of the world's largest tracksites indicates that they have all been documented and in most cases discovered only recently. A "large" tracksite is arbitrarily defined as one in which at least 1000 tracks or about 100 trackways are mapped or reliably documented. In ascending stratigraphic order these large sites include:

Age	Site Name and Location	# Tracks	Trackways	Reference
Up Cret	Toro Toro, Bolivia	—	~ 100	Leonardi 1984
Up Cret	Lark Quarry, Australia	> 4000	> 500	Thulborn and Wade 1984
Lr Cret	Peace River, Canada	~ 1200	~ 100	Currie 1983
Lr Cret	Jindong, South Korea	—	~ 250	Lim et al. herein
Lr Cret	Nei-Monggol, China	~ 1000	—	(Rong 1985)*
Lr Cret	Piau, Brazil	—	~ 150	Leonardi 1984
Up Jura	Purgatoire, USA	~ 1300	~ 100	Lockley et al. 1986
Up Jura	Mt Kugitang-Tau, USSR	~ 2700	—	(Romashko 1986)*
Mid Jura	Salt Valley, Utah	> 1000	> 100	Lockley and Gillette herein
Mid Jura	Chaoyang, China	~ 4000	—	(Zhen et al. 1983)
Lr Jura	Rocky Hill, USA	~ 1000	—	Ostrom 1968
Up Trias	Peacock Canyon, USA	—	~ 100	Conrad et al. 1987

(* indicates brief and uncertain documentation)

The statistics listed above indicate that, in the last decade alone, tens of thousands of tracks, comprising hundreds of distinct trackways, have been mapped, counted or otherwise documented from only a handful of the larger known sites. There exist a bigger number of sites where

several hundred tracks comprise trackways numbering in the dozens. When included with all known sites the available ichnological record of dinosaur footprints must approach hundreds of thousands of tracks representing evidence of the activity of tens of thousands of animals.

Such statistics, although impressive, are not particularly surprising. An individual animal was presumably capable of leaving hundreds or even thousands of footprints in environments where reasonable fossilization potential existed. It may also have laid eggs by the dozens. However, the same individual could never contribute more than one skeleton to the fossil record.

One outcome of the resurgence of dinosaur ichnology has been a significant accumulation of new data on a variety of Mesozoic tracks. This data can be compared and integrated with information derived from other field research for an improved understanding of dinosaur paleobiology. As suggested by Lockley (1986), ichnological data can contribute to an understanding of dinosaur paleobiology in many areas including behavior (locomotion, speed, social behavior), paleoecology (relative abundance, dinosaur community composition and diversity), paleobiogeography (latitudinal and paleoenvironmental range) and biostratigraphy (evolutionary longevity). As outlined below, ichnological data can also have interesting paleoenvironmental implications.

Before analyzing dinosaur behavior on the basis of trackway evidence, it is important for the ichnologist to be reasonably sure of the trackmaker's affinity. There were a number of important non-dinosaurian trackmakers which left footprints in the Mesozoic record. Some of these produced tracks which have proved controversial. At present about seven localities are known to yield true bird tracks. These are all Cretaceous in age and all represent discoveries which postdate 1930. Because the tracks all bear such a striking resemblance to modern birds, with high divarication angles of 110°–120° between digits II and IV, they have generally not been misidentified. However, in a reversal of the 19th century pattern, some have been incorrectly assigned to dinosaurs. Others remain problematic (Parker and Balsley this volume). Non-dinosaurian archosaurs and other reptiles have proved more problematical. Crocodilian tracks appear to have been interpreted as pterosaurian in origin on many occasions (Padian and Oisen 1984, Unwin this volume, Prince and Lockley this volume) but in other cases may be genuinely attributable to pterosaurs (Gillette and Thomas this volume). In one instance a turtle trackway has been interpreted as that of a hopping dinosaur (Thulborn this volume). It appears that other tracks, e.g., those of mammals (Sarjeant and Thulborn 1986), lepidosaurs and mammal-like reptiles are generally very rare and poorly preserved during most of the age of dinosaurs, particularly in the Jurassic and Cretaceous.

There are at least two important reasons that help explain the rarity and problematic nature of non-dinosaurian ichnites in the Mesozoic. Firstly non-dinosaurian trackmakers were generally small, at least after the Late Triassic. This means that there is a bias against

the preservation of their tracks, whereas dinosaurs included many large species whose tracks were obvious and easily preserved (Lockley and Conrad this volume). The second point pertains to the different habits of terrestrial, aquatic and airborne creatures. We might expect that the tracks of swimmers and fliers are relatively rare in comparison with those of terrestrial walkers, although for fliers this may be a function of low diversity in the Mesozoic. The trackways of swimmers and fliers may also be much less complete, and, in the case of swimmers, modified by water action. While the size-related bias in favor of the preservation of large tracks is similar to the taphonomic biases affecting the skeletal record, ethological or behavioral biases represent specific group-related phenomena that are likely to be expressed differently in the ichnological and body fossil record. The difference in frequency between the traces and skeletal remains of aquatic and terrestrial animals is a good example. Terrestrial tracks may significantly outnumber body fossil remains, whereas the reverse appears to hold true for aquatic animals.

Although dinosaur egg material was discovered in Europe in the late nineteenth century, it was not until the 1920's that the Mongolian nest site discoveries confirmed that dinosaurs laid eggs in well ordered nests. As was the case in the history of footprint ichnology, the initial discoveries were followed by a lull. During this time, material came to light only sporadically. However, in the field of egg and nest research there has also been a dramatic resurgence of activity in recent years. Discoveries of large sites have been made in North America (Horner 1987), China (Mateer this volume) and on the Indian subcontinent (Hirsch this volume, Jain this volume, Sahni this volume), as well as at previously known localities in Europe. Collectively the sites reveal a variety of distinctive egg types based on microstructure and macrostructure, some of which can be assigned to specific dinosaurian egg layers on the basis of associated embryos. Others, however, are of unproven affinity and not necessarily dinosaurian in origin. The situation closely parallels the current state of knowledge in footprint ichnology, where considerable progress has been made. Many important questions have been answered but much still remains to be discovered.

While there remains considerable untapped material in the fields of track and egg site ichnology, the field of coprolite research remains largely unexplored and the potential unknown. As indicated by Jain (this volume), coprolites are very abundant locally.

Footprint Paleobiology

(i) Behavior

Dealing first with strictly behavioral aspects of paleobiology we note that tracks are unequivocal evidence of the posture and locomotion of the trackmaker. The erectness of a particular group or its inclination towards digitigrade or plantigrade stance, or bipedal versus quadrupedal progression is clearly indicated by the trackways (e.g., Wade this volume, Kuban this volume). Incorrect postural

reconstructions can not be adhered to in the face of contrary trackway evidence.

In particular, dinosaur trackways provide evidence that dinosaurs stood and walked erect. Among bipedal trackways attributed to both theropods and ornithopods, feet were placed one in front of another leaving a narrow parasagittal trackway (Fig. 0.2). Pace angulation values are high and pes tracks invariably overlap the trackway midline to some degree. The main differences between trackways of bipedal ornithopods and theropods include: (i) foot shape, with toes generally more slender in theropods, (ii) degree of pedal rotation, with inward (positive) rotation more pronounced in ornithopods, and (iii) step and stride length generally shorter in ornithopods.

Generally bipeds were digitigrade. However, a number of examples exist of obligatory or facultative bipeds which left tracks and trackways exhibiting distinct metatarsus impressions (Fig. 0.3). This suggests that occasional plantigrade progression was employed by a variety of different theropods and ornithopods. The reasons for this are open to speculation but may have been a behavioral response to soft substrate conditions, or a function of changing from bipedal to quadrupedal progression (slowing, sitting, squatting or stalking). Such tracks provide useful information on metatarsus dimensions.

Trackways of large quadrupeds, including sauropods, ceratopsians, ankylosaurs and certain large ornithopods also indicate erect posture. However, the trackways are generally somewhat wider than those of bipeds of comparable size. In all cases the pes tracks are larger than the manus prints (heteropody), with the disparity being most pronounced in sauropods and ornithopods. Usually the pes tracks overlap the trackway midline, although this is not always the case. Invariably however, the manus tracks exhibit higher pace angulation values and are usually situated anterolaterally with respect to the pes. This evidence suggests that in general the front limbs hung vertically from the shoulder girdle or diverged slightly, while the hind limbs converged slightly beneath the body.

Tracks have also been used to derive speed estimates. The whole debate over dinosaur speeds has been quite lively and need not be reviewed here in detail (see Thulborn this volume). In essence, the ichnological record indicates that the vast majority of dinosaurs whose tracks are preserved were walking. A number of authors have pointed out that this is to be expected — animals do not expend energy unnecessarily. However a few examples of running dinosaurs do exist (Farlow 1981, Thulborn this volume), indicating that small bipeds were fleet of foot and that larger theropods attained speeds of about 30–40 km/hr. Trackways indicating rapid progression by large quadrupedal dinosaurs have yet to be documented. This should not be taken as an indication that these animals could not run. Rather it indicates that they ran infrequently, and that the probability of finding "maximum speed trackways" is very remote. The converse of this assumption is that data on walking dinosaurs is very abundant, allowing for the compilation of reliable statistics for this mode of progression (Thulborn this

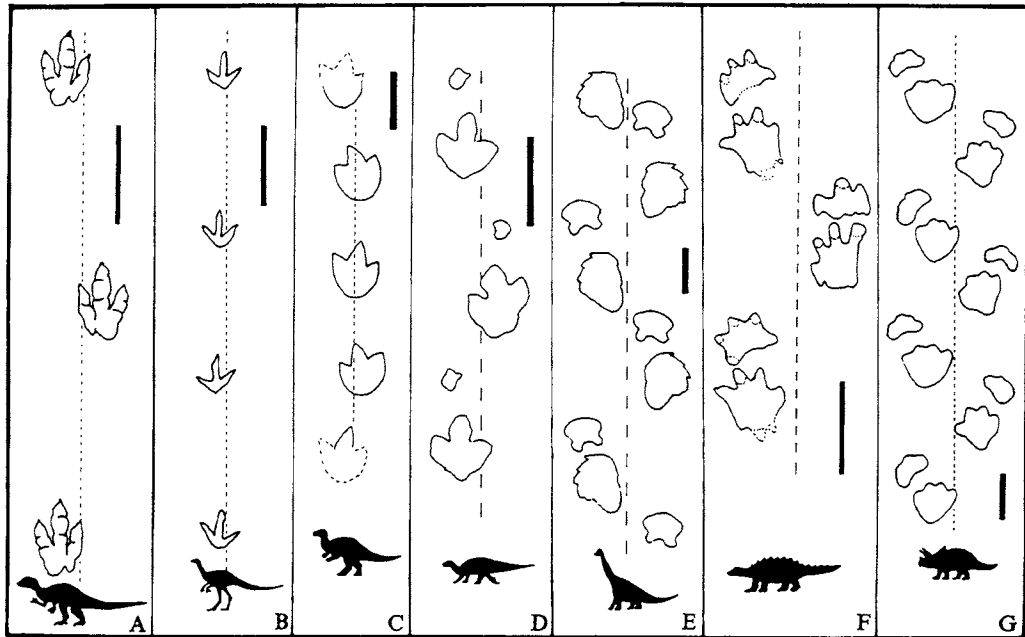


Figure 0.2. Representative dinosaur trackways. A–C, bipeds; D–G, quadrupeds. A, *Eubrontes* after Lull (1953). B, unnamed coelurosaur. C, unnamed ornithomimid. D, *Caririchnium* (B–D) after Lockley (1987). E, *Brontopodus* after Bird (1944). F, *Tetrapodosaurus* after Sternberg (1932). G, unnamed ceratopsian trackway after Lockley (1988). Dotted lines indicate trackway midline. Scale bars = 50 cm.

volume).

(ii) Paleoeecology

In the realm of paleoeecology it is becoming increasingly clear that ichnofaunas can give insight into the composition and diversity of dinosaur communities in particular areas. As data accumulates to suggest that footprint assemblages, like other faunas, are facies related, it is clear that paleoeecological census data derived from tracksites is intricately related to patterns of paleobiogeographic distribution (Leonardi this volume, Lockley and Conrad this volume).

The simplest examples of the application of ichnological data in paleoeecological census studies are cases where distinctive tracks are known in otherwise unfossiliferous deposits. Here the ichnofauna is the only paleontological data available. However, many other examples exist in which the ichnofauna contributes a proportion of our knowledge on the composition of a fauna in a particular area or deposit.

The issue of the relative importance of trace and body fossils in such situations has led to two serious misconceptions: (i) that tracks do not occur in the same deposits as body fossils, and (ii) that tracks are only really important in situations where body fossils have not been found.

The first misconception is generally unfounded.

Although there are many trackbearing stratigraphic units that lack abundant body fossils, there are a large number of instances of substantial ichnofaunas originating from fossiliferous beds. For example, in the Late Triassic of North America and Europe, large ichnofaunas occur in association with diverse body fossil assemblages. The same is true for later Mesozoic deposits like the Morrison Formation of North America, the Wealden of Europe and a number of Late Cretaceous deposits in the Rocky Mountain region.

Having recognized that important trace and body fossil assemblages do co-occur, the question arises as to how well the different data sets correspond. If the tracks indicate a faunal assemblage which is similar to that derived from skeletal remains, the track data might be considered redundant, especially if it was discovered afterwards. Such a superficial approach should be discouraged because it ignores a number of important paleoeecological and taphonomic considerations. An ichnofauna that is compatible with the skeletal record confirms that minimal taphonomic biases exist, and affords an opportunity to study the fauna in the dynamic context of trackmaking activity. It may also provide relative abundance data not available from the skeletal record.

In instances where the ichnofauna supplements the faunal data derived from the body fossil record, an obvious paleontological benefit accrues. However, the additional data do more than just enlarge the faunal list. They sug-

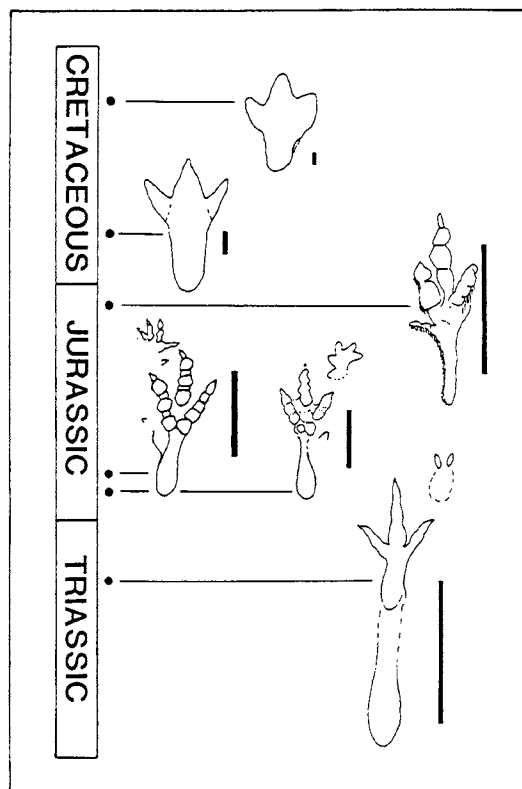


Figure 0.3. Dinosaur tracks exhibiting metatarsus impressions. *Agialopus* from the Late Triassic of Colorado. *Anomoepus* from the Lower Jurassic of New England (left) and southern Africa (right), *Jialingpus* from the Upper Jurassic of China, unnamed theropod from the Lower Cretaceous of Texas and "Dinosauropodes," a hadrosaurian ichnite from the Late Cretaceous of Colorado. Scale bars = 10 cm.

gest the degree to which the skeletal record is incomplete and the probable nature of associated taphonomic biases. In the Popo Agie Formation of Colorado and Wyoming for example, an ichnofauna of small vertebrate and invertebrate traces exists in association with a skeletal record that only records the presence of a few large vertebrates. Apart from tripling the overall faunal list, the ichnofauna indicates a strong bias against preservation of the small vertebrate fauna in the skeletal record.

Because ichnofaunas are the *in situ* traces of animal activity, a strong case can be made in favor of their use in paleoecological census estimates. In the case of the Popo Agie fauna cited above, we can speak with some confidence of a fauna dominated by non-dinosaurian mesovertebrates and estimate the dinosaurian component as only a minimal proportion (about 5%, see Lockley and Conrad this volume). Whenever a large ichnofauna is known, the potential exists to estimate the composition of the fauna with some accuracy. Generally the data derived from this exercise conform with known patterns of faunal distribution, thus inspiring confidence in the ichnofaunal census method.

We do not claim that ichnofaunas can not be misleading. They may, for example, reflect the activity of a particular group in a particular setting rather than the overall composition of the fauna in a given region. Theropod abundance may appear over-represented because members of this group were more active than species in other niches. However, as data accumulate, consistent patterns do emerge. For example, the majority of Cretaceous ichnofaunas are dominated by large ornithopods (Lockley and Conrad this volume) and occur in lithosomes representing lowland, humid coastal plain settings. By contrast the theropod-sauropod ichnofaunas appear to be associated with semi-arid low latitude settings. Similar paleogeographic patterns are also noted elsewhere in the Mesozoic (Leonardi this volume).

(iii) Evolution

Finally in the area of biostratigraphy it is now possible to trace many of the major phases of dinosaur evolution through the ichnological record. Demathieu (this volume) has demonstrated that early dinosauroid forms emerged as early as the Middle Triassic, at which time they represented only a small proportion (about 3–5%) of the fauna. In the Late Triassic–Early Jurassic transition, clear ichnological changes are seen and can be used for biostratigraphic correlation on a global scale (Olsen and Galton 1984). Whereas Late Triassic ichnofaunas are characterized by chirothere tracks and various other distinct forms like *Atreipus* and the ubiquitous *Rhynchosauroides*, the Early Jurassic is characterized by an abundance of grallatorid tracks (*Grallator* and *Anchisauripus*) in association with distinctive forms like *Anomoepus* and *Batrachopus*. The rise of sauropod faunas in the Jurassic is also now discernible in the ichnological record (Monbaron et al. 1985), as is the distinctive transition to faunas dominated by large ornithopods in the Cretaceous (Lockley and Conrad this volume).

Paleoenvironmental Implications of Dinosaur Footprint Ichnology

In addition to being used for an improved understanding of dinosaur paleobiology, tracks may also be used to help interpret paleoenvironments. For example, the depth of tracks is an indication of the water content of sediments. Employing such a simple observation, we can use track depth to help determine the position of shorelines or paleogradients between firm dry ground and moist ground or bodies of water. In other words, they may be "paleo water-table" indicators.

Dinosaurs had considerable impact on the substrates over which they passed. While firm substrates resisted disturbance, soft yielding substrates were particularly susceptible to deformation. The resulting vertebrate bioturbation or "dinoturbation" is therefore a function of both paleobiological and paleoenvironmental factors. While the density and degree of activity of the dinosaur population represent contributing paleobiological factors, it is physical paleoenvironmental factors that ultimately determine the

character of the impacted sediment. For example, extensive and heavily bioturbated or "dinoturbated" beds generally occur at lithological boundaries and imply long exposure to trampling rather than sudden influx of dense dinosaur populations.

Despite being widespread, "dinoturbation" has received little serious scientific attention and has often been overlooked or misinterpreted as soft sediment deformation of non-biogenic origin. As sedimentologists, stratigraphers and paleontologists look more closely at Mesozoic terrestrial successions, an increasing number of dinoturbated beds have been recognized, particularly in Late Jurassic through Late Cretaceous formations. Preliminary indications suggest that vertebrate bioturbation reached a Phanerozoic peak at this time due to the extensive impact of large gregarious herbivores, particularly sauropods, iguanodontids and hadrosaurs. Dinoturbated beds may be relatively localized in association with playa and larger perennial lake deposits; however, it may also be prevalent in coastal lowland lithosomes where extensive deposits are accumulating at base level. Because dinoturbation may radically alter sediments leading to their mixing and homogenization, the phenomenon should be of particular interest to soft rock geologists concerned with the interpretation of terrestrial deposits.

Paleobiological and Paleoenvironmental Aspects of Egg and Nestsite Ichnology

From a paleobiological perspective, egg and nest sites also provide important information about (i) behavior, (ii) paleoecology, and (iii) evolution. Interpretations of dinosaurian behavior based on egg and nest site discoveries have proved quite dramatic. Dinosaurs apparently laid eggs in an orderly fashion, sometimes in neat spiral arrangements or linear rows. Clutch size was also quite specific for certain groups. Another aspect of nest site behavior which has attracted much attention is the parental care scenario. This was first hinted at by the discovery of *Protoceratops*, the inferred egg layer, locked in a fatal struggle with *Velociraptor*, the presumed egg thief. Subsequent work by Horner (1987) and his colleagues has produced further evidence of parental care and protection at nest sites. Horner's work has also indicated that dinosaurs nested in colonies, sometimes sharing a site among several species, and that they returned to these chosen sites over extended periods of time. Similar "site fidelity" is also suggested by multiple nest bearing layers in China (Mateer this volume) and India (Jain this volume).

The choice of specific paleogeographic locations for nest sites may account, to some degree, for certain dinosaur distribution patterns. The rarity of small dinosaurs, whether real or perceived, in any given deposit or area, may relate to the location of nest colonies as much as to other factors such as preservation or population dynamics.

The evolution of the hard-shelled egg was a major evolutionary accomplishment, facilitating the diversification of reptilian faunas in Permo-Triassic terrestrial habitats. However, few diagnostic eggs are known before the Late

Mesozoic. By this time they are morphologically distinct, like the dinosaurs that laid them.

Elongated ornithopod eggs appear to be quite distinct from the large subspherical eggs attributed to sauropods. Differences in external ornament and microstructure are also analogous to shell structure differences seen in different invertebrate classes. Because egg remains are less abundant than tracks, and associated only with reptiles and birds, it is not yet possible to discern with confidence major evolutionary events by analysis of existing egg fossils (Hirsch this volume). However, as information accumulates, there is no reason to doubt that eggshell studies will add to our knowledge of the evolution of dinosaurs, other reptiles and birds.

Summary

Dinosaur tracks and traces form a major and often spectacular part of the vertebrate ichnological record. Tracks outnumber egg and coprolite remains and provide important information on morphology gait, speed, dinosaur paleoecology and habitat zonation. Egg and nest remains provide specific information on hatchling morphology, colonial nesting strategies and parental care. Coprolites remain problematic and poorly documented despite their potential for analyzing dinosaurian diets.

Viewed in the broad context of vertebrate (tetrapod) ichnology, dinosaur tracks and traces are more abundant than those attributed to other classes, either during the "Age of Dinosaurs" (Middle Triassic to Late Cretaceous) or at other times. There are several explanations for this situation. In Late Paleozoic through Earliest Mesozoic time (Late Devonian to Middle Triassic), following the first appearance of land-based tetrapods, ichnites consist mainly of tracks, with few confirmed reports of eggs, nests or coprolites. Initially also trackmakers were small and confined to lowland humid paleoenvironments, thus minimizing their impact. With the Permo-Triassic radiation of reptiles, tracks become more diverse and abundant, but reports of other ichnites remain scarce.

By Jurassic and Cretaceous times, the evolution of dinosaurs resulted in a significant increase in vertebrate bioturbation. "Dinoturbation" reached a peak. Egg and nest sites also become more abundant at this time, presumably reflecting a better preservation potential for large and strategically located eggs than for the smaller and less robust eggs that were probably produced by dinosaur predecessors.

Following the demise of the dinosaurs there is a distinct shortage of vertebrate ichnites in the early part of the Age of Mammals. The reasons for this are fairly obvious and relate to the impoverishment of tetrapod faunas and the sharp reduction in egg laying groups. Despite the increased abundance of fossil ichnites in the latter part of the Age of Mammals, there is little doubt that dinosaur tracks and traces are an unusually important and abundant part of the overall ichnological record. They have also been studied with increasing intensity in recent years and are now understood in much greater depth.

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